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Influence of Environmental Factors on Color Change in the Lizard, Anolis carolinensis

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INFLUENCE OF ENVIRONMENTAL FACTORS ON COLOR CHANGE IN THE LIZARD, *ANOLIS CAROLINENSIS*

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This thesis is submitted in partial fulfillment of

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ABSTRACT

An analysis has been attempted of the relationship of five factors (temperature range, light duration, background color, eye condition and time of day) reported to influence color change responses in Anolis carolinensis. Three temperature ranges, three light durations, two background colors, and two eye conditions have been used. Anoles were blinded by administering an electric spark to the eye. The diurnal periodicity factor was assessed by observing the anoles once every three hours for a twenty-four hour period.

Two approaches to the analysis of the data have been tried - one of statistical analysis via computer programming and one of induction by the examination of the raw data.

The diurnal periodicity factor is suggested not to be present in either intact or blinded anoles. Other factors seem to play roles of importance in this order: 1) eye condition, 2) temperature range, 3) light duration, and 4) background color, in both intact and blinded anoles. From the inductive approach the order is the same as above, except that the importance of temperature varied, which may have been due to inconsistency in the high temperature stimulus.

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INTRODUCTION

The color changes of the anole, Anolis carolinensis, have interested investigators for forty years. Color changes within Anolis carolinensis, an Iguanid lizard, are thought to be completely under hormonal control. Kleinholz (1938a) who did the classical work with this animal showed by extraction and injection experiments that the pituitary excitant involved in darkening Anolis is from the intermediate lobe of the pituitary. In his recent review, Waring (1963) supports this work and states that there have been no suggestions that this excitant is other than MDH (melanocyte-dispersing hormone). In a more recent review, Fingerman (1965) reverts to the older, more generalized terminology: "Intermedin darkens Anolis; hypophysectomy results in permanent pallor." Pallor (green color) may be due to cessation of MDH in circulation or to the presence of a second pituitary hormone, as yet unidentified.

Environmental factors are known to influence the skin color of A. carolinensis. Both Waring (1963) and Fingerman (1965) have written reviews helpful in deciphering the many color change studies that have been done.

Most workers agree that the prime factors in eliciting color change responses in A. carolinensis are those of illumination and temperature. A. carolinensis is the only

described animal having dominant pituitary coordination of chromatic response which exhibits a complete pallor, ie., green color, in darkness (Kleinholz, 1938a; Hadley, 1931; Waring, 1963). A. carolinensis is brown under laboratory conditions of moderate temperature (18-28°C.) and light (Kleinholz, 1938a; Rahn, 1956).

The response to background color in A. carolinensis is unmistakable. Investigators agree that dark lizards turn green when placed on a brightly illuminated white background; green lizards become brown when placed on an illuminated black background (Kleinholz, 1938a). In Kleinholz' experiments, normal green animals turned brown within 22 minutes when placed on an illuminated black background; normal brown lizards turned green within approximately 30 minutes when placed on an illuminated white background (Kleinholz, 1938a).

The above mentioned responses to background color may be modified by temperature extremes. Hadley (1931) found in intact A. iodurus that high temperatures cause the melanophores to contract while low temperatures cause them to expand. Hutchison and Larimer (1960) reported that intact A. carolinensis were green at high temperatures, under conditions of stress, or with no illumination, and were dark chestnut with illumination. Rahn (1956) reported that animals became lighter with increased body temperatures and suggested this to be a factor which intensified the adrenalin release.

Cold extremes are not as great a threat to lizards as heat extremes. "Prolonged temperatures below freezing point are probably lethal, but above this lizards can exist in a state of suspended activity for long periods." (Bellairs, 1957). Tests with A. iodurus (Hadley, 1931) suggested that low temperatures were conducive to the dark state. Hutchinson and Larimer (1960) reported that at low temperatures A. carolinensis are usually dark, the color not being influenced by light.

A final complicating factor is one of diurnal periodicity, reported by Rahn and Rosendale (1941). Anolis (species not identified), usually brown under influence of light and bright green at night, when exposed to continuous light on a white background at 22°C and 40°C for up to four days, turned green during the corresponding night period and brown during the day. Anolis placed in continuous darkness for eight and eighteen days at a temperature range between 22-24°C turned green during the solar night and (up to 90% of them) brown during the solar day. These results suggest that the diurnal periodicity factor overrides the otherwise expected responses to background, high temperature and lack of illumination. Rahn and Rosendale (1941) conclude that the pars intermedia of the pituitary releases a hormone in diurnal cycle, which release is independent of photoreceptors, but normally reinforced by the alternating day and night period. Waring (1963) discussed this work and commented that no observations were recorded for eyeless ani-

mals. This present study is intended to help answer the question of the function of photoreceptors in diurnal periodicity in color responses. If this response is independent of photoreception, this would not be in agreement with the hypothesized stimulus pathway through the eye for MDH release from the amphibian and fish pituitary.

Waring (1963) gives (after Hogben and Slome, 1936) a picture of events occuring during physiological background response. He suggests "B" and "W" areas of the retina; illumination of the "B" area evoking MDH secretion into the bloodstream, hence the black background response. Illumination of the "W" area of the retina would either reduce the secretion of MDH (according to the one-hormone hypothesis) or cause secretion of a melanin-aggregating hormone (according to the two-hormone hypothesis). In either case circulating MDH would be destroyed by peripheral tissues and by the liver upon cessation of stimulation to the retina.

When surveying literature about "blinded Anolis carolinensis one must note the manner in which the anoles were blinded. Wilson (1939) reported that if a black hood were fitted over the eyes (and the parietal eye in some cases), A. carolinensis turnes brown. This may have been a response to the perception of illuminated black rather than effective blinding, ie., disruption of the optic tract. The experimental procedure, however, was not described in sufficient detail to allow an adequate judgement.

Kleinholz (1938a) cauterized the eyes of hos experimental animals. Wilson (1940) "blinded" lizards by gluing the eyelids together with a mixture of charcoal and celloidin. Here it is possible that the animals which turned green did so as a result of their eyelids becoming, at least in part, unglued.

Blindfolded - or blinded - Anolis carolinensis show no response to background color but do show typical responses to light and darkness (Wilson, 1940; Kleinholz, 1938a). Illuminated, blinded anoles turned green in an average of 22.4 minutes (Kleinholz, 1938a). Waring (1963) suggests:

> Darkening of eyeless animals brought from darkness to light is a coordinated response dependent on extra-optic reception and pituitary mediation. The speed of response is similar to that recorded when intact animals are reacting to the background.... The location of the receptors and the precise route whereby the pituitary is influenced have not been determined.

Wilson's (1940) tests with A. carolinensis showed the typical darkening in response to light. These anoles with celloidin-glued eyelids required various strengths and durations of illumination for this response to occur. If only one side of the lizard were illuminated, that side only turned brown. Under 16 foot-candles (ft-c.) of illumination for 16 hours, seven blinded A. carolinensis showed these results: in 2 minutes all were brown; in 20 minutes one of these had turned green; in 4 hours a second one had turned green; and in

16 hours a third had turned green.

Wilson (1940) also reported that high temperatures with light induced green coloration in blindfolded A. carolinensis . At 44°C the anoles were brown; when exposed to 50°C they turned green; they died if the temperature much exceeded 50°C. Thus the high temperature capable of eliciting a color response would appear to lie between 44° and 50° C. The 44°C and 50°C were evidently body temperatures, as the room temperature varied between 30° and 33°C. Wilson found found temperature to be an overriding agent, as blindfolded Anolis were always green above 44°C and brown below 13°C. This contrasts with Zoond and Eyre's (1934) work with chameleons. Zoond and Eyre reported from their extensive experimentation with chameleons that exposure to cold did not induce darkening. Temperatures down to 1°C (which render the animal comatose) did not stop the pallor response to darkness. In comparing these two animals one must remember that the chameleon's color is under a different mediation than that of Anolis. However, Waring (1963) was sufficiently concerned by this difference in response to suggest that Wilson's work needs independent confirmation.

As stated above, low temperatures are conducive to the dark phase in Anolis. Reports have indicated that this response is not dependent on illumination (Hutchinson and Larimer, 1960; Hadley, 1931). When Wilson (1940) put blindfolded anoles (green phase) into a dark refrigerator at 10°

to 13° C, most turned brown and remained brown while in the refrigerator. Those not completely brown after 12 hours turned brown when the temperature was lowered to 9-10°C. Some that had been brown turned partially or completely green if maintained for awhile at 13°C. This suggests that 13°C may be the temperature at which the low temperature response in darkness is attained, ie., from normal green to low temperature brown. In light (15 ft-c.) and at low temperatures (ice was packed around the anoles' containers), the animals all turned brown and remained brown during the two hours for which these conditions were maintained.

This summary has shown that much of the reported data concerning the color changes of Anolis carolinensis are fragmentary or unclear. This study was undertaken to correlate five of the factors known to affect color change in A. carolinensis: temperature, illumination, background color, diurnal periodicity, and effective blinding. This correlation will be helpful in evaluating previous literature, since it suggests an hierarchy of importance of these factors in eliciting color change responses under laboratory conditions.

METHODS AND MATERIALS

The animals used in this study were adult male Anolis carolinensis obtained commercially from The Snake Farm, LaPlace, La. These animals were housed individually in 21 cm. x 15 cm. x 13 cm. clear plastic terraria (Beco, Inc.) furnished with red plastic top, clear plastic water dish and brown and green plastic perches. These cages afforded social contact through visual stimulation without allowing for either injury through possible conflict or development of the social hierarchy characteristic of their group behavior. Also, each animal could be satisfactorily maintained on mealworm larvae (Tenebrio sp.) and water, on a three-day feeding cycle. On the first day, (usually between 9:00 A.M. and 12:00 noon), the anoles were given water and one to several mealworm larvae; on the second day water was offered by squirting it into the cage; on the third day neither food nor water was offered.

The laboratory room in which the animals were maintained had an average air temperature of $22 \pm 4^{\circ}C$. Lighting conditions included diffuse light from overhead fluorescent tubes with an average table-top intensity of 2-3 ft-c. Heat lamps provided strong, direct light from 12:00 noon to 4:00 P.M. (E.S.T.) daily. Table 1 gives the temperature gradient within a laboratory cage under heat lamps and

under overhead illumination. This table also shows the gradients of light intensity within a laboratory cage under these two lighting conditions. It should be noted, however, that the lizard was free to select a range of temperature within the cage by hiding under wood shavings or on the backside of the perches. The pimpled plastic floor of each cage was covered with a small amount of wood shavings to help absorb waste material; the wood shavings were changed as necessary.

Animals selected for experimental use were first observed under laboratory conditions once every three hours for a twenty-four hour period, and then placed under experimental conditions. This entailed the following: the animals were removed from their cages and placed in experimental cages which were the same as laboratory cages except that the inside ceiling, floor and three walls, water dish and perches had been painted with either white or black flat enamel. One end of the cage was left clear to allow for light penetration. The experimental lizards were supplied with water but no mealworm larvae, then placed into an incubator between 9:00 P.M. and 12:00 midnight of the first day of the three-day feeding cycle. They were allowed 48 hours of acclimation to the experimental conditions, then tested during the third twenty-four hour period. The experimental animals were watered on the first day of acclimation and left undisturbed on the second, except in the tests run at high temperatures, in which cases

it was necessary to provide water on all three days.

Incubator lighting was provided by three two-foot, 15 watt fluorescent tubes, so spaced horizontally on the rear wall of the incubator, that each provided light for one of the three shelves in the incubator; each cage received the same amount of illumination. See Table 2 for light intensity values within the experimental cage. Temperature varied to some extent within the incubator; this information is given in Table 3.

Figure 1, the experimental flow chart, shows the light and temperature variables chosen. The 12 hours of light in that condition were from 9:00 A.M. to 9:00 P.M. The blinded animals were rendered so by administering an electric spark to the eye from an electric needle. Animals thus treated were tested for blindness by macroscopic observation of the eyes (whether they were sealed over or clouded, indicating extensive protein denaturation) and also by noting characteristics of behavior. Anolis is very skittish and jumps about if a foreign object is brought near the eyes. A pencil-like object was waved past the eyes of blinded animals before they were placed under experimental conditions; this procedure was often followed during the test and usually after the test, especially if the test had been run at an extreme temperature. Any animal responding to this stimulus was not used in experiments, or data from it used in analyses.

A sample size of nine proved most convenient with the

materials at hand. Insofar as possible, the lizards were tested in a predetermined pattern, ie., test conditions 1, 7, 13, 19, 25, 31 - or any such sequence or use. (Refer to Figure 1.) In general, by following such a sequence, light and background factors were held constant, a procedure chosen to give greater uniformity in response, possibly ruling out the elusive factor of individual variability.

Observations were made within an experimental enclosure housing the incubator and observation table. This enclosure was a 6 ft x 6 ft. x 5 ft. wooden frame covered with canvas and black paper, providing a comfortable and sufficiently light-free working space. Observations of the experimental animals were made once every three hours for a twenty-four hour period beginning at 12:00 midnight at the end of the second day of test conditions and ending at 9:00 P.M. the next evening. The caged anoles were removed from the incubator one at a time. The animal was compared to a standard color chart (Grumbacher, Inc., "The Color Key") and returned to the cage and incubator-all usually within 30 seconds. The color chart was illuminated with a small fluorescent lamp, the light intensity from which averaged 36 to 40 ft-c. The readings were taken in such a way as to assure maximum uniformity in handling and observation. Records were kept of the animals color, the temperature within the experimental enclosure, certain behavioral characteristics, the approximate handling time, and whether the anole showed either before or

during handling the mottled condition indicative of stress (post orbital patches turning black, sometimes accompanied by a dark mid-dorsal pattern).

Objective techniques for color determination were not found, though the author considered spectrophotometer reflectance attachments, light meters, and photography.

The data were made quantitative by coding each of the nine colors (selected on the basis of similarity to the anoles' colors), in the following way. The nine colors (see Figure 2) were ranked in order, lightest green to darkest brown. The quantitative symbol for an observation consisted of two digits: the first represented the predominant color of the anole; the second represented any patch or shading of different color appearing on the dorsal surface of the trunk excluding the mid-dorsal pattern, if present. Thus a reading of 38 would represent a green anole with brown patches, while a 33 would indicate that the anole was uniformly green.

It should be mentioned that the color chart used ("The Color Key", Grumbacher, Inc.) was printed on paper and thus is not necessarily consistant in its manufacture. Colors in enamel paints would have been a better tool in this regard.

The data were analyzed by an IBM 1620 computer, using these programs: for within group regression, program 06.0.080 from the 1620 General Program Library; for homogeneity of variance within groups, program 06.0.081 from the 1620

General Program Library; for the Friedman two-way analysis of variance, program 06.0.203 of the 1620 General Program Library; for analysis of correlation of time intervals and eye condition with color response, and for all other analyses of variance as presented herein, Analysis of Variance program (VIMS, 1966), written by F.J. Wojcik and adapted to the needs of this study by R.E. Smith.

TABLE 1

LABORATORY ENVIRONMENT

The first number in the cells below is the light in foot-candles as measured with a Wesson light meter, while the second is the temperature in degrees Centigrade, as measured with a Yellow Springs Instruments telethermometer. The room temperature was 20°C. The abbreviation O.H. refers to the overhead fluorescent lighting; H.L. refers to the illumination from the heat lamps.

Shelf posotion	End of cage closest to heat lamps		End of cage farthest from heat lamps		Center of cage	
	H.L. + O.H.	O.H. only	H.L. + O.H.	O.H. only	H.L. + O.H.	O.H. only
Bottom	240 25	10 19	140 24	5 19	200 27	20 19
Middle	720 26	15 19	200 36	5 19	290 30	10 19
Top	290 30	15 19	20 28	10 19	120 29.5	20 19

TABLE 2

EXPERIMENTAL ENVIRONMENT

This table shows the light variation within incubators used in the experiment as measured from the middle position of the middle shelf of the incubator. All intensities are in foot-candles, as measured with a Wesson light meter.

Position of sensing device	Incubator I		Incubator II	
	White Box	Black Box	White Box	Black Box
End of box closest to mounted lights	400	300	440	410
End of box farthest from mounted lights	160	20	160	40
Middle of box	200	70	200	110
Floor of box	180	60	195	70

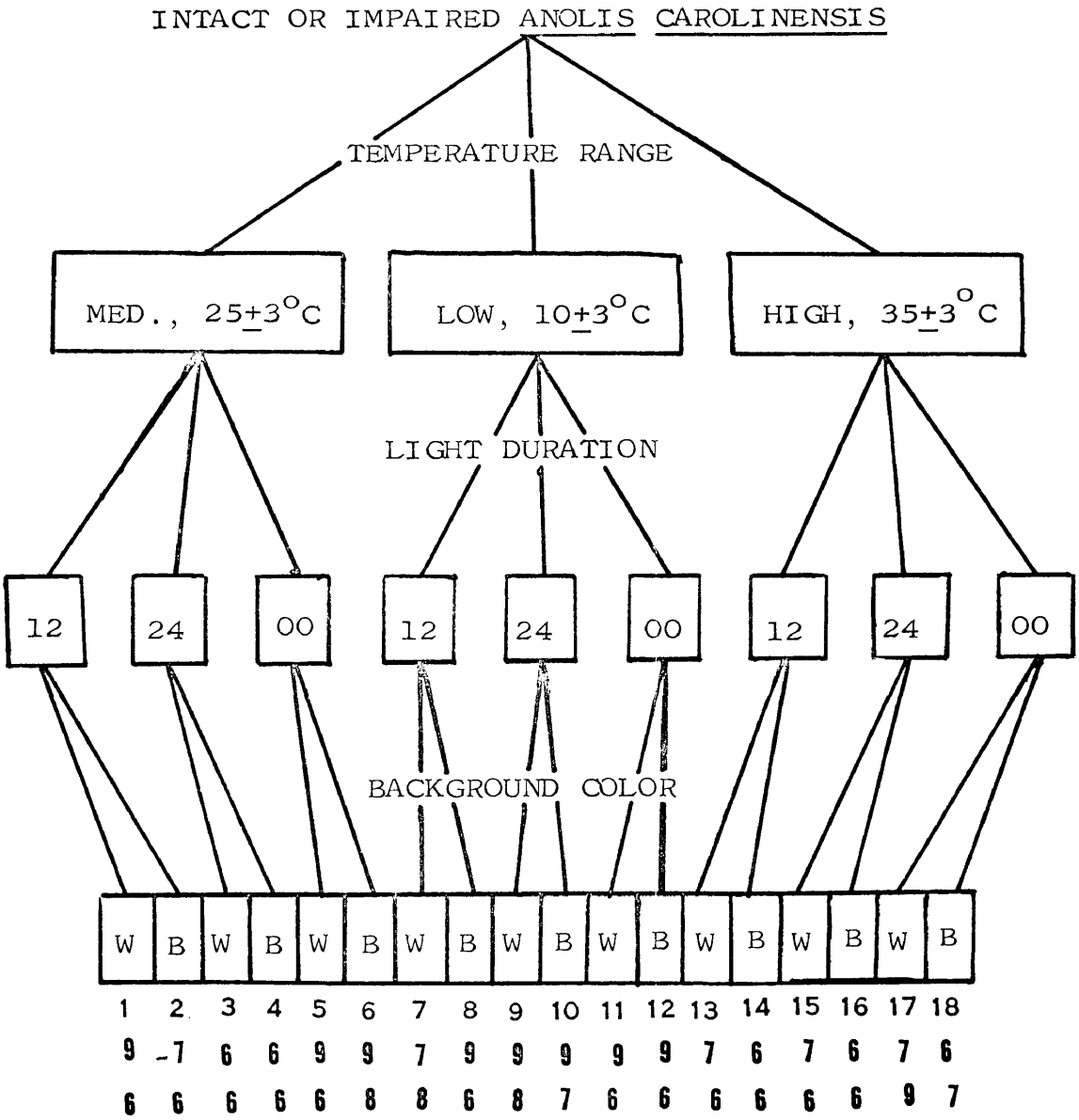
TABLE 3

EXPERIMENTAL ENVIRONMENT

This table shows temperature variation due to temperature range differences and position within the incubator. A Yellow Springs Instruments telethermometer with nine thermisters was used, except in certain cases in Incubator 2, as noted below*, in which one thermometer in an experimental box was moved from position to position. The numbers represent positions within the incubator, from the top left to the bottom right corners.

	HIGH RANGE		MED. RANGE		LOW RANGE	
Position	B*	W	B*	W*	B	W
Incubator 1						
1	-0.75	-1.00	-0.50	+0.50	+1.13	+1.10
2	+0.25	-0.25	+1.25	+2.00	+2.50	+2.10
3	+0.30	-0.40	+1.25	+1.75	+3.00	+2.37
4	-1.50	-0.75	0.00	+0.75	+2.50	+0.63
5	-1.50	-0.50	+0.50	+1.00	+3.50	+1.37
6	-1.50	-0.13	+o.75	+2.25	+4.00	+1.87
7	-0.90	-0.50	-0.25	+1.12	+2.50	+0.63
8	-1.50	-0.13	0.00	+1.25	+2.75	+1.37
9	-0.75	-0.13	+0.60	+1.50	+4.00	+1.87
Incubator 2						
1	-0.25	0.00	-0.50	-0.50	+0.10	+1.00
2	+1.75	-0.50	-0.25	0.00	+0.75	+1.00
3	0.00	-0.25	-0.75	+1.00	+0.25	+0.50
4	+0.50	-1.50	-1.00	+0.50	+1.20	+1.00
5	+1.75	-3.50	+0.25	+0.50	+0.90	+1.00
6	-0.25	-2.00	+0.50	+2.00	+1.10	+2.00
7	-2.75	+1.00	0.00	+0/50	+0.80	+2.00
8	-1.50	-1.00	+0.50	+0.50	+1.00	+2.00
9	-3.00	-0.50	+2.75	+2.50	+0.50	+1.00

Figure 1. Experimental flow chart. The following chart summarizes the experiment in that it shows how the five environmental factors were manipulated to permit a series of thirty-six unique tests. The twelve hours of light in the 12 condition were from 9:00 A.M. to 9:00 P.M. Within the background variable, W indicates white and B indicates black. The first row of numbers listed is the identification number of the test; the tests using impaired (blinded) animals were numbered in the same sequence as those using intact animals. The second row gives the sample size for the tests using intact animals; the third row gives this information for tests using impaired animals.


INTACT OR IMPAIRED ANOLIS CAROLINENSIS
TEMPERATURE RANGE
MED., 25±3°C
LOW, 10±3°C
HIGH, 35±3°C
LIGHT DURATION
12
24
00
12
24
00
12
24
00
BACKGROUND COLOR
W B W B W B W B W B W B W B W B W B
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
9 7 6 6 9 9 7 9 9 9 9 9 7 6 7 6 7 6
6 6 6 6 6 8 8 6 8 7 6 6 6 6 6 6 9 7

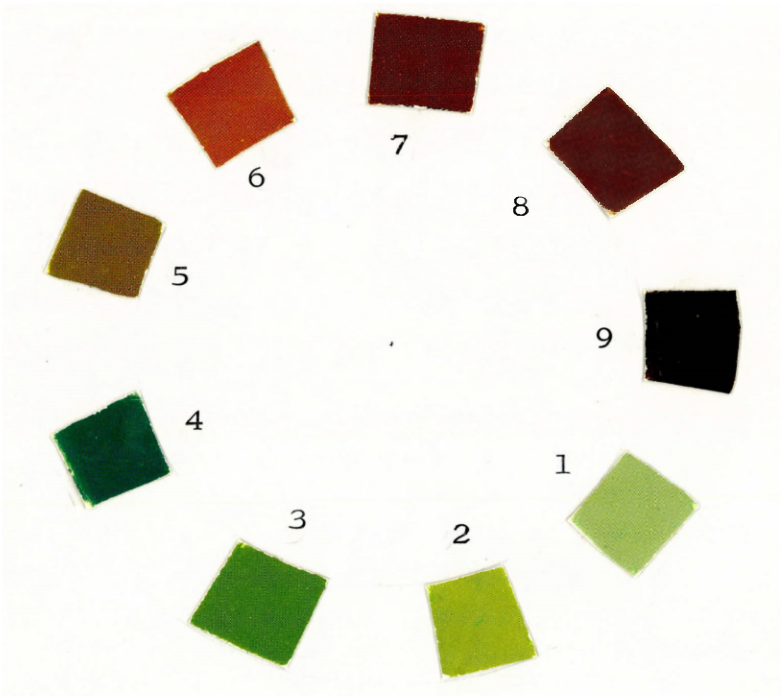


Figure 2. This color wheel, comprised of colors from "The Color Key" (Grumbacher, Inc.), indicates the derivation of the coding used for experimental observations.

RESULTS AND DISCUSSION (1)

A statistical study was undertaken in the hope that the results of various analyses of variance would indicate the relative significance of the five factors under consideration. There is one known bias in the data; the 6:00 A.M. observations were occasionally omitted and data from these tests were handled as follows. Those anoles showing no change between 3:00 A.M. and 9:00 A.M. readings were used in preference to those showing a change. The 6:00 A.M. reading was given the same numerical code as the 3:00 A.M. and the 9:00 A.M. readings, based on the assumption that the anoles had not changed color during that time. This assumption was supported when several of these tests were repeated using the same anoles, and the 6:00 A.M. reading taken.

Three basic tests were used in these analyses of variance. To determine whether the $\underline{F}$ test or the $\underline{t}$ test was to be used in analyzing the variance of the test data, a preliminary analysis of the variances was computed, comparing in each case the greater to the lesser value. If the value was 1 or close to 1 (ie., homogeneity or nonsignificance of variance) the computer proceeded to an analysis of variance by computing the $\underline{F}$ value. The $\underline{F}$ test here, a ratio of the

variance between samples to the variance within samples, was considered significant at the 90% level of confidence. If the preliminary test on the variances showed them to be heterogeneous (significant), a t test was used, the t value being determined significant at the 95% confidence level. The t test measures the degree of statistically significant difference of the means. Statistical tables from Snedecor (1956) were used. (See Appendix II for the computer program used.)

Tests of within-group regression showed a strong linear relationship within test groups of both intact and blinded anoles (Appendix III), indicating that each of the 36 test groups was self-consistent.

The Friedman two-way analysis of variance, a non-parametric test, was used to rank means and variances of the readings from intact and blinded anoles. Results (Table 4) show that the means of readings at 12:00 A.M. and 9:00 P.M. rank higher in blinded anoles, while in intact anoles the means ranked lower for these same two times. This would indicate that blinded anoles were darker in the late P.M. adn early A.M. hours, while intact anoles were lighter during the same time. There was no rank variation with time in the variances of either the intact or blinded anoles. However, those of the intact anoles were consistently higher than those of the blinded anoles. It must be noted that causitive factors other than time and

eye condition were ignored in these tests.

Correlation of each test time with all others were computed to attempt to show the possibility of a diurnal periodicity factor. The following table (Mack, p.156, 1960) was used to assign the strength of r, the correlation coefficient:

Qualitative meaning of r	
± r	Clustering tendency of population about a straight line
0.0 to 0.2	No tendency
0.2 to 0.5	Weak
0.5 to 0.7	Moderate
0.7 to 0.9	Strong
0.9 to 1.0	Very strong

Results (Table 5) indicate that intact anoles show no differences in strength of correlation values with time interval differences, while blinded anoles do show some differences. This would indicate the possibility of a diurnal periodicity factor in color response of blinded anoles only, since r was consistently strong in each case on intact anoles and variable in blinded anoles. It might be noted that the "strong" correlations in blinded anoles and "very strong" in intact anoles of the 3:00 A.M. to 6:00 A.M. and 6:00 A.M. to 9:00 A.M. readings would be due at least in part to the arbitrarily assigned values to the 6:00 A.M. readings, as mentioned above.

These findings augment but do not agree with those of Rahn and Rosendale (1941) who suggested a strong (overriding) diurnal periodicity in intact anoles at medium temperatures in both continuous light and continuous darkness, and at high temperatures in continuous light. It is possible that ignoring factors other than eye condition and time resulted in some masking effect; however, inspection of the data (Appendix I) would lead one to conclude that there is no diurnal periodicity factor in the color response of intact anoles. It is difficult, too, to conclude that this factor is operative in blinded anoles, as there are no distinctively recognizable patterns of diurnal response, and also because means of each group at each time interval indicate consistency through the testing period. The effects of mechanical injury and physiological upset resulting from the blinding technique were impossible to isolate because of the design of the experiment. These also may have influenced color response. Blinding these anoles by severing the optic tract was not attempted; this procedure might possibly have given more precise results.

In the comparison of the other factors, two approaches were tried. (All analyses following were done according to the computer program found in Appendix II.) In the first approach, the time factor was ignored, all eight readings being considered in the analysis. Each of the remaining four factors of eye condition, temperature range, light duration and background color was tested against the

other three. For example, if background responses were investigated, test 1 would be compared to test 2, etc. (Refer to Figure 1.) The results from this approach are in Tables 6, 7, 8 and 9. As mentioned above, for the purposes of this report unless otherwise noted, F was considered significant at the 90% confidence level, while t was considered significant at the 95% level of confidence and highly significant at the 99% confidence level. The t tests which were not significant at the 95% confidence level were also not significant at the 90% confidence level, except in two cases noted bleow.

The results of tests of the effect of eye condition (Table 6) show that the preliminary test of variance were significant in every case; the t tests were highly significant in those cases using equal sample sizes. This points out the fact that the t test is much more sensitive when equal samples are used; it is possible that significance was masked in the other t tests because of unequal sample sizes. Results of tests shown in Tables 7, 8 and 9 indicate nonsignificant t or F values in each case. These results indicate that in each case the experimental groups are from the same population (ie., the null hypothesis is accepted). Or, in biological terms, the factor under consideration (light duration, temperature range or background color) was not shown to be a significant causative factor in eliciting color change responses.

There are several possible reasons for the negative

results obtained with blinded animals. One possibility is that the fluorescent lights did not emit light of the appropriate wavelength in sufficient intensity to elicit a response. Although responses were obtained with intact animals (Appendix 1), it is known that stronger illumination is required to elicit a response in blinded anoles than in intact ones (Waring, 1963). It is unfortunate that most workers have not provided information on light intensity.

A second possible reason for the lack of significance is that the response to light is masked when data from eight time periods are considered together. This possibility has been tested by rerunning several of the tests, using only data from the 12:00 noon readings. The results are given in Tables 10, 11 and 12. Results (Table 10) of the effect of background color for both intact and blinded anoles showed the following:

In intact anoles:

1) at medium temperatures $\underline{t}$ was significant at 12 hours light duration and highly significant at continuous darkness. $\underline{F}$ was highly significant at continuous light.
2) at low temperatures $\underline{t}$ was highly significant at 12 and 24 hours light duration.
3) at high temperatures $\underline{t}$ was highly significant at 24 hours light duration.

In tests with blinded animals $\underline{t}$ was significant at high temperatures, continuous darkness and $\underline{F}$ was highly

significant at high temperatures, continuous light.

Results in Table 10 indicate that intact anoles respond to background, whereas blinded anoles for the most part do not. It is notable that three tests (intact anoles) were significant at medium temperature range, while two were significant at low and one at high, and also that the only two cases of significant response in blinded anoles occured at high temperatures. This indicates that temperature extremes may override otherwise occurring responses to background. In regard to light duration, tests on intact anoles at continuous light were consistently significant, while tests at 12 or no hours light varied in consistency of significance. Continuous exposure to stimulus would enforce the response, producing these expectable results. Light duration would seem to be less important in blinded anoles.

Results of tests (Table 11) showing the effect of temperature were as follows:

In intact anoles:

1) comparisons of medium to low temperatures showed t highly significant in tests done in continuous darkness, white and black backgrounds.
2) in low to high temperature comparisons t was highly significant at 12 hours light duration on a white background, and significant at continuous light on a black background. F was

significant at no light on a black background.

3) in medium to high temperature comparisons *t* was significant at continuous light on a white background.

In blinded anoles:

1) comparing medium to low temperature ranges, *t* was significant at the 90% confidence level at 12 hours light duration on a white background

2) comparing low to high temperature ranges, *t* was significant at continuous light, white and black backgrounds, and at no light, black background.

3) comparing medium to high temperature ranges, *t* was highly significant at continuous light on a white background and significant in continuous light on a black background.

The results given above (and in Table 11) indicate no consistent ranking of factors. However, it is interesting to note the parallel of response between blinded and intact anoles in comparisons 2) and 3) above.

Table 12 gives the results of tests on the effect of light duration on color response.

In intact anoles:

1) at medium temperatures *t* was significant at 0 to 12 hours light duration, white background. *F* was significant at 12 to 24 hours light duration, black background.

2) at low temperatures *t* was significant at 0 to 24 hours light duration, white background, and 0 to 12 and 12 to 24 hours light duration, black background.

3) at high temperatures *t* was significant at 0 to 24 hours light duration, white background, while *F* was significant at 0 to 24 hours light duration, black background.

In blinded anoles:

1) at medium temperatures no tests were significant.

2) at low temperatures *t* was highly significant at 12 to 24 hours light duration, white background, and significant at 0 to 12 hours light duration, white background.

3) at high temperatures *t* was highly significant at 12 to 24 hours light duration, white background and black background, and significant at 0 to 24 hours light duration, white and black backgrounds.

The results as given in Table 12, considered in regard to the number of significant cases at each temperature range, background condition and light duration, would indicate that temperature range is more important than light duration, which, in turn, is more important than background color in eliciting color responses in these anoles. This would be true for both intact and blinded anoles, though

most of the significant responses in intact anoles were at the low range, while most of the significant responses in blinded anoles were at the high temperature range.

TABLE 4

FRIEDMAN TWO-WAY ANALYSIS OF VARIANCE

This table gives the ranking of the means and variances of blinded and intact anoles at each of the eight observation times.

Time	Means		Variances	
	Blind	Intact	Blind	Intact
12:00 A.M.	2.00	1.00	1.00	2.00
3:00 A.M.	1.00	2.00	1.00	2.00
6:00 A.M.	1.00	2.00	1.00	2.00
9:00 A.M.	1.00	2.00	1.00	2.00
12:00 P.M.	1.00	2.00	1.00	2.00
3:00 P.M.	1.00	2.00	1.00	2.00
6:00 P.M.	1.00	2.00	1.00	2.00
9:00 P.M.	1.00	1.00	1.00	2.00

TABLE 5

CORRELATION COEFFICIENTS OF COLOR RESPONSE

The results below show the comparisons of each of the eight observation times with each of the others. The relative strengths of the correlations are assigned according to Mack, 1960. (See text, p.156.)

Time	r, Blind	Strength
12 A.M. to 3 A.M.	0.58	Moderate
12 A.M. to 6 A.M.	0.62	Moderate
12 A.M. to 9 A.M.	0.54	Moderate
12 A.M. to 12 P.M.	0.40	Weak
12 A.M. to 3 P.M.	0.41	Weak
12 A.M. to 6 P.M.	0.33	Weak
12 A.M. to 9 P.M.	0.37	Weak
3 A.M. to 6 A.M.	0.76	Strong
3 A.M. to 9 A.M.	0.65	Moderate
3 A.M. to 12 P.M.	0.43	Weak
3 A.M. to 3 P.M.	0.52	Moderate
3 A.M. to 6 P.M.	0.39	Weak
3 A.M. to 9 P.M.	0.46	Weak
6 A.M. to 9 A.M.	0.82	Strong
6 A.M. to 12 P.M.	0.55	Moderate
6 A.M. to 3 P.M.	0.52	Moderate
6 A.M. to 6 P.M.	0.45	Weak
6 A.M. to 9 P.M.	0.41	Weak
9 A.M. to 12 P.M.	0.60	Moderate
9 A.M. to 3 P.M.	0.52	Moderate
9 A.M. to 6 P.M.	0.50	Moderate
9 A.M. to 9 P.M.	0.49	Weak
12 P.M. to 3 P.M.	0.68	Moderate
12 P.M. to 6 P.M.	0.67	Moderate
12 P.M. to 9 P.M.	0.69	Moderate
3 P.M. to 6 P.M.	0.68	Moderate
3 P.M. to 9 P.M.	0.62	Moderate
6 P.M. to 9 P.M.	0.66	Moderate

TABLE 5, (cont.)

Time	r, Intact	Strength
12 A.M. to 3 A.M.	0.89	Strong
12 A.M. to 6 A.M.	0.86	Strong
12 A.M. to 9 A.M.	0.77	Strong
12 A.M. to 12 P.M.	0.72	Strong
12 A.M. to 3 P.M.	0.76	Strong
12 A.M. to 6 P.M.	0.79	Strong
12 A.M. to 9 P.M.	0.75	Strong
3 A.M. to 6 A.M.	0.92	Very strong
3 A.M. to 9 A.M.	0.89	Strong
3 A.M. to 12 P.M.	0.77	Strong
3 A.M. to 3 P.M.	0.77	Strong
3 A.M. to 6 P.M.	0.80	Strong
3 A.M. to 9 P.M.	0.79	Strong
6 A.M. to 9 A.M.	0.91	Very strong
6 A.M. to 12 P.M.	0.78	Strong
6 A.M. to 3 P.M.	0.73	Strong
6 A.M. to 6 P.M.	0.81	Strong
6 A.M. to 9 P.M.	0.75	Strong
9 A.M. to 12 P.M.	0.86	Strong
9 A.M. to 3 P.M.	0.82	Strong
9 A.M. to 6 P.M.	0.83	Strong
9 A.M. to 9 P.M.	0.84	Strong
12 P.M. to 3 P.M.	0.85	Strong
12 P.M. to 6 P.M.	0.84	Strong
12 P.M. to 9 P.M.	8.83	Strong
3 P.M. to 6 P.M.	0.85	Strong
3 P.M. to 9 P.M.	0.85	Strong
6 P.M. to 9 P.M.	0.85	Strong

TABLE 6

EFFECT OF EYE CONDITION

The first column gives the test numbers, the first of which (intact) was compared to the second (blinded). The sample number is given by n; total data pieces is 8n, as all eight observations were read as data. If the comparison of variances was significant at the 90% confidence level (FVAR +), *t* was computed; if not (FVAR -), *F* was determined.

Tests	n	FVAR	*F*	*t*
1, 1	9,6	+		0.93
2, 2	7,6	+		0.95
3, 3	6,6	+		-52.01**
4, 4	6,6	+		-48.57**
5, 5	7,6	+		0.93
6, 6	9,6	+		0.92
7, 7	7,8	+		0.76
8, 8	9,6	+		0.92
9, 9	9,8	+		0.75
10,10	9,7	+		0.82
11,11	9,6	+		0.92
12,12	9,6	+		0.92
13,13	7,6	+		0.96
14,14	6,6	+		-51.44**
15,15	6,6	+		-55.04**
16,16	6,6	+		-53.27**
17,17	7,9	+		0.73
18,18	6,7	+		0.87

**significant at the 99% level of confidence

TABLE 7

EFFECT OF BACKGROUND

The first column gives the tests compared, the first to the second. The first nine comparisons are for intact anoles; the second nine are for blinded anoles. The second column gives the sample size of the test group; total data pieces would be 8n, as all eight observation times were used. If the comparison of variances was significant (FVAR +), the *t* test was computed; if not, (FVAR -), the *F* value was determined.

Tests	n	FVAR	*F*	*t*
1, 2	9,7	-	0.01	
3, 4	6,6	-	--	
5, 6	9,9	-	--	
7, 8	7,9	-	--	
9,10	9,9	-	--	
11,12	9,9	-	--	
13,14	7,6	-	--	
15,16	6,6	-	--	
17,18	7,6	-	--	
1, 2	6,6	-	--	
3, 4	6,6	-	--	
5, 6	6,8	-	--	
7, 8	8,6	-	0.01	
9,10	8,7	-	--	
11,12	6,6	-	--	
13,14	6,6	-	--	
15,16	6,6	-	--	
17,18	9,7	-	0.01	

Where no *F* is given, the value was less than 0.005.

TABLE 8

EFFECT OF TEMPERATURE

The first column gives the tests compared, the first to the second. The first eighteen comparisons are of intact anoles; the second eighteen are of blinded anoles. The second column gives the sample size of the test group; total data pieces would be 8n, as all eight observations were used. If the comparison of variances was significant (FVAR +), the *t* test was computed; if not, (FVAR -), the *F* value was determined.

Tests	n	FVAR	*F*	*t*
1, 7	9,7	-	0.05	
2, 8	7,9	-	0.01	
3, 9	6,9	-	0.04	
4,10	6,9	-	0.03	
5,11	9,9	-	0.04	
6,12	9,9	-	0.04	
7,13	7,7	-	0.08	
8,14	9,6	-	0.08	
9,15	9,6	-	0.06	
10,16	9,6	-	0.07	
11,17	9,7	-	0.13	
12,18	9,6	-	0.09	
1,13	9,7	-	--	
2,14	7,6	-	0.03	
3,15	6,6	-	--	
4,16	6,6	-	0.01	
5,17	9,7	-	0.03	
6,18	9,6	-	0.02	

TABLE 8 (cont.)

Tests	n	FVAR	*F*	*t*
1, 7	6,8	-	--	
2, 8	6,6	-	0.04	
3, 9	6,8	-	0.01	
4,10	6,7	-	0.01	
5,11	6,6	-	0.01	
6,12	8,6	-	0.04	
7,13	8,6	-	0.02	
8,14	6,6	-	0.06	
9,15	8,6	-	0.03	
10,16	7,6	-	0.04	
11,17	6,9	-	0.10	
12,18	6,7	-	0.07	
1,13	6,6	-	0.01	
2,14	6,6	-	--	
3,15	6,6	-	0.01	
4,16	6,6	-	0.01	
5,17	6,9	-	0.05	
6,18	8,7	-	0.05	

Where no *F* is given, the value was less than 0.005.

TABLE 9

EFFECT OF LIGHT

The first column gives the tests compared, the first to the second. The first eighteen comparisons are for intact anoles; the second eighteen are for blinded anoles. The second column gives the sample size of the test groups; total data would be 8n, as all eight of the observations for each anole were used. If the preliminary comparison of variances was significant (FVAR +), the *t* test was computed; if not, (FVAR -), the *F* value was determined.

Tests	n	FVAR	*F*	*t*
5, 1	9,9	-	0.07	
1, 3	9,6	-	0.04	
5, 3	9,6	-	0.19	
6, 2	9,7	-	0.03	
2, 4	7,6	-	0.09	
6, 4	9,6	-	0.22	
11, 7	9,7	-	0.05	
7, 9	7,9	-	0.06	
11, 9	9,9	-	0.23	
12, 8	9,9	-	0.07	
8,10	9,9	-	0.08	
12,10	9,9	-	0.29	
17,13	7,7	-	0.02	
13,15	7,6	-	0.03	
17,15	7,6	-	0.10	
18,14	6,6	-	0.03	
14,16	6,6	-	0.05	
18,16	6,6	-	0.16	

TABLE 9, (cont.)

Tests	n	FVAR	*F*	*t*
5, 1	6,6	-	0.01	
1, 3	6,6	-	0.02	
5, 3	6,6	-	0.06	
6, 2	8,6	-	0.01	
2, 4	6,6	-	--	
6, 4	8,6	-	0.03	
11, 7	6,8	-	0.03	
7, 9	8,8	-	0.01	
11, 9	6,8	-	0.06	
12, 8	6,6	-	0.01	
8,10	6,7	-	0.03	
12,10	6,7	-	0.08	
17,13	9,6	-	--	
13,15	6,6	-	0.02	
17,15	9,6	-	0.02	
18,14	7,6	-	--	
14,16	6,6	-	0.02	
18,16	7,6	-	0.04	

Where no *F* is given, the value was less than 0.005.

TABLE 10

EFFECT OF BACKGROUND

The first column gives the tests compared, the first to the second. The first nine comparisons are of intact anoles, the second nine, of blinded anoles. The second column gives the sample size of test groups which also equals the total data pieces, as these are based on 12:00 P.M. data only. If the comparison of variances was significant (FVAR +), the *t* test was computed; if not (FVAR -), the *F* value was determined.

Tests	n	FVAR	*F*	*t*
1, 2	9,7	+		2.26*
3, 4	6,6	-	11.67**	
5, 6	9,9	+		-11.89**
7, 8	7,9	+		0.89
9,10	9,9	+		-14.70**
11,12	9,9	+		6.70**
13,14	7,6	+		0.92
15,16	6,6	+		-25.27**
17,18	7,6	-	0.02	
1, 2	6,6	-	0.59	
3, 4	6,6	-	0.02	
5, 6	6,8	-	--	
7, 8	8,6	+		0.87
9,10	8,7	-	0.44	
11,12	6,6	-	2.76	
13,14	6,6	-	0.30	
15,16	6,6	-	8.64**	
17,18	9,7	+		2.16*

Where *F* is not given, the value was less than 0.005.
*indicates significance(95% confidence)
*indicates high significance (99% confidence)

TABLE 11

EFFECT OF TEMPERATURE

The first column gives the tests compared, the first to the second. The first eighteen comparisons are of intact anoles,the second eighteen, of blinded anoles. The second column gives the sample size of test groups which also equals the total data pieces, as these tests are based on 12:00 P.M. data only. If the comparison of variances was significant (FVAR +), the *t* test was computed; if not, (FVAR -), the *F* value was determined.

Tests	n	FVAR	*F*	*t*
1, 7	9,7	+		0.65
2, 8	7,9	-	1.72	
3, 9	6,9	+		0.90
4,10	6,9	-	0.63	
5,11	9,9	+		-189.34**
6,12	9,9	+		-56.13**
7,13	7,7	+		33.75**
8,14	9,6	-	0.19	
9,15	9,6	+		2.17*
10,16	9,6	-	1.43	
11,17	9,7	+		0.55
12,18	9,6	-	11.38**	
1,13	9,7	+		0.75
2,14	7,6	-	0.88	
3,15	6,6	+		7.35**
4,16	6,6	-	0.14	
5,17	9,7	+		0.45
6,18	9,6	+		0.87

TABLE 11,(cont.)

Tests	n	FVAR	F	t
1, 7	6,8	+		2.05***
2, 8	6,6	-	0.97	
3, 9	6,8	-	--	
4,10	6,7	-	0.74	
5,11	6,6	-	1.28	
6,12	8,6	+		0.57
7,13	8,6	+		0.77
8,14	6,6	-	0.27	
9,15	8,6	+		2.37*
10,16	7,6	+		2.45*
11,17	6,9	-	0.01	
12,18	6,7	+		2.37*
1,13	6,6	-	1.89	
2,14	6,6	-	2.75	
3,15	6,6	+		-11.23**
4,16	6,6	+		2.57*
5,17	6,9	-	1.36	
6,18	8,7	+		0.44

Where no F is given, the value was less than 0.005.
*indicates significance (95% confidence)
** indicates high significance (99% confidence)
*** indicates special significance (90% confidence)

TABLE 12

EFFECT OF LIGHT

The first column gives the tests compared, the first to the second. The first eighteen comparisons are of intact anoles; the second eighteen are of blinded anoles. The second column gives the sample size of test groups which also equals the total data pieces, as these tests are based on 12:00 P.M. data only. If the comparison of variances was significant (FVAR +), the *t* test was computed; if not, (FVAR -), the *F* value was determined.

Tests	n	FVAR	*F*	*t*
5, 1	9,9	+		-10.85**
1, 3	9,6	+		0.69
5, 3	9,6	+		0.58
6, 2	9,7	+		0.72
2, 4	7,6	-	5.52*	
6, 4	6,6	+		0.95
11, 7	9,7	+		0.71
7, 9	7,9	-	0.88	
11, 9	9,9	+		21.47**
12, 8	9,9	+		12.54**
8,10	9,9	+		-12.55
12,10	9,9	-	--	
17,13	7,7	+		7.20**
13,15	7,6	-	0.64	
17,15	7,7	+		2.31*
18,14	6,6	-	0.77	
14,16	6,6	-	0.87	
18,16	6,6	-	3.53*	

TABLE 12, (cont.)

Tests	n	FVAR	F	t
5, 1	6,6	-	0.54	
1, 3	6,6	-	1.40	
5, 3	6,6	-	3.08	
6, 2	8,6	+		0.57
2, 4	6,6	-	0.15	
6, 4	8,6	+		0.57
11, 7	6,8	+		2.06***
7, 9	8,8	+		-12.90**
11, 9	6,8	-	1.12	
12, 8	6,6	-	0.05	
8,10	6,7	-	0.05	
12,10	6,7	-	--	
17,13	9,6	-	1.03	
13,15	6,6	+		-8.49**
17,15	9,6	+		2.31*
18,14	7,6	+		0.81
14,16	6,6	+		-8.06**
18,16	7,6	+		2.45*

Where no value is given for F, the value is less than 0.005.

*indicates significance (for F, at the 90% level of confidence; for t, at the 95% confidence level

**indicates high significance (99% confodence level)

***indicates special significance, t at the 90% confidence level

RESULTS AND DISCUSSION (2)

Because of the insensitivity of the statistical tests (on unequal sample sizes) an inductive consideration of the results (Appendix II) was undertaken for purposes of comparison with the statistical results.

Intact anoles. At moderate temperatures A. carolinensis are reported to be green on an illuminated white background, brown on an illuminated black background, and green in darkness regardless of background (Hadley, 1931; Kleinholz, 1938; Waring, 1963). The results of this study are for the most part in agreement with these reports. During tests (12 and 24 hours light duration) on white background the anoles were green; on illuminated (12 hours duration) black background there was a mixed response - some anoles being green, some brown, and some green with brown patches. However, in continuous light (black background) the anoles were brown as reported in the literature. In darkness (duration 12 and 24 hours) these anoles were consistently green. The factor of diurnal periodicity as reported by Rahn and Rosendale (1941) was not observed (see test data 3, 4, 5 and 6, Appendix I).

Results of low temperature tests on illuminated white and black backgrounds as well as tests in darkness on both white and black backgrounds (see tests 7 through 12,

Appendix I) showed most anoles to be brown under all of these conditions. These results are in agreement with those of Hutchison and Larimer (1960), that A. carolinensis are brown at low temperatures regardless of light; no tests of effect of background or time of day were reported.

The results of tests at high temperatures were neither as uniform nor as conclusive as the preceding. Anoles are reported to be green at high temperatures (Hutchison and Larimer, 1960). Background, light duration and diurnal periodicity factors have not been considered in the literature. Data from tests 12 through 18 (Appendix I) indicate at least a partial response to illuminated background, as anoles on an illuminated (12 and 24 hours duration) white background were green, while anoles on an illuminated black background showed a mixed response. Those subjected to 12 hours light duration showed green, brown, and green with brown patches responses, while those in continuous light were predominantly brown. In tests run in darkness the majority of anoles were green as would be expected, due to factors of both high temperature and darkness. In this regard, it is difficult to explain the results of tests 17 and 18 in which some anoles were brown.

There are several possible reasons for these mixed responses. A. carolinensis, being under greater stress at high than low temperatures, would be expected to show less consistency at high than at low temperatures. Also, there

might have been more response to handling, though efforts were made to reduce this factor to a minimum. Mention might also be made that the temperature range used in this study was necessarily approximately 10°C less than that used by Wilson (1940). It is possible that in cases of brown color at high temperatures, the stress was not sufficient to induce the change to green, which change Wilson noted to occur at about 44°C.

From examination of the results in intact anoles only. it is possible to rank the four factors that are included in this part of the investigation. From the results at moderate temperatures, it appears that light overrides background response. There is no evidence for diurnal periodicity. At low temperatures it appears that temperature overrides the light factor in importance, that light is more important than background, and that the diurnal periodicity factor is unimportant. Thus in a numerical order, these would be 1) temperature, 2) light duration, 3) background color, and 4) diurnal periodicity (if operative). At high temperatures the order is somewhat modified. Here it appears that background overrides the temperature response, producing a ranking of: 1) light duration, 2) background, 3) temperature, and 4) diurnal periodicity (if operative).

Blinded anoles. Blinded A. carolinensis at moderate temperatures are reportedly brown in light and green in darkness, showing no response to background differences

(Kleinholz, 1938a). The effects of light duration and time of day have not been reported. Data on blinded anoles (tests 1 through 4, Appendix I) show that most of these blinded anoles were indeed green with both 12 and 24 hours of darkness.

Wilson's (1940) report that A. carolinensis were consistently brown below 13°C was not supported by the results of this investigation. Anoles at low temperatures (both white and black backgrounds) with 12 and 24 hours light duration were predominantly green (see data from tests 7 through 10, Appendix I). In darkness (see data from tests 9 through 12, Appendix I) the majority of anoles with 12 hours light duration were green; in continuous darkness there was a mixed, inconclusive response on white background, while on the black background the majority of the anoles were brown. Since perception of background was supposedly not possible due to factors of blindness and darkness, it seems reasonable to consider these two background conditions together and conclude that the trend was toward brownness at low temperatures in darkness.

At high temperatures (12 and 24 hours light duration) the results (see data from tests 13 through 16, Appendix I) show anoles to be brown on both white and black backgrounds. In darkness the tendency was toward green, though in some tests (see data from tests 17 and 18, Appendix I) the results were mixed.

The results of this investigation lead to the conclusion that a diurnal periodicity was not present . An analysis by inspection of the ranked importance of the other factors considered in the experiment lead to these conclusions. At moderate temperatures, test results show that light duration is a factor of greater importance than background color. At low temperatures, light duration still overrides the background response, but the role of temperature is inconclusive. In one situation the light duration seems to override temperature, while in another situation the opposite is true. At high temperatures the hierarchy is: 1) light duration, 2) temperature range, 3) background (if operative).

The overriding importance of light as a factor in determining color response in these anoles leads to one of three conclusions: 1) the lizards were not blinded, 2) the lizards can percieve light via extra-optic receptors, or 3) the lizard can detect the heat given off by the lamps when operating, and respond to this temperature change. The first possibility is considered unlikely, since tests for blindness showed that the anoles did not respond to objects moved in front of them (see METHODS). This does not rule out the possibility that the animals retained a low-level optic sensitivity to light, however. The third is not a feasible explanation, as the heat emitted by the fluorescent light was neglible. The anoles could select a range of temperatures within the experimental cage that

was probably more variable than the variation due to any heat given off by the fluorescent lights. Thus the second possibility is accepted as the most feasible explanation for this phenomenon. This is not a new finding; extensive discussion is found in Waring (1963).

This inductive approach has substantiated the statistical treatment, except in one point, the importance of temperature.The statistical results showed temperature to be second in ranked importance after eye condition. Here in intact anoles high temperature range was not as important as background color (ie., ranked fourth), while in blinded anoles high temperature was third in importance after light duration.

SUMMARY

1. Factors of temperature range, background color, light duration, eye condition and time of day have been considered in regard to elicitation of color response in adult male Anolis carolinensis.
2. Data were subjected to statistical analyses and computer analyzation.
3. Each of the 36 test groups was self consistent, as shown by within-group regression analyses.
4. The Friedman two-way analysis of variance rankings and the correlation of groups at different time intervals indicate the possibility of some fluctuation of color response with time in blinded anoles. However, none of the means of these groups show significant change with time. In any case, a strong overriding diurnal periodicity as reported by Rahn and Rosendale (1941) in intact anoles was not observed in this study.
5. Eye condition is an isolating factor in color response in some cases. The author believes that more significant results would have been obtained, had the sample sizes been equal.
6. In tests of the importance of background color, eye condition overrides background color. In intact anoles

temperature is more important than is background; in blinded anoles, temperature is more important than is light duration.

7. In tests of the importance of temperature range, the following ranking of factors held for both intact and blinded anoles: 1) temperature, 2) light duration, 3) background color.

8. A synthesis of the results above would give this ranking of the factors: 1) eye condition, 2) temperature range, 3) light duration, and 4) background color.

9. These results were substantiated by the inductive examination of the raw data, except in one point. In intact anoles high temperature range ranked fourth in importance after background color; in blinded anoles high temperature ranked third in importance after light duration.

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LIST OF APPENDICES

APPENDIX I

RAW DATA

These data presented in tabular form are a combination of the environmental conditions and coded observations. The hyphenated heading number is composed of (from left to right): the test number (1 to 18), the background color (1 = white, 2 = black), the temperature range (10, 25, or 35) in degrees Centigrade, the eye condition (1 = intact, 2 = blinded), and the light duration (10, 12 or 24) in hours. The columns contain the following information: the first column indicates whether the animal was obviously stressed during the test (0 = not stressed, 1 = stressed), the second column is the identifying number of the test animal, and the third through the eleventh columns are the coded observations for each of the eight time intervals, beginning at 12:00 midnight and ending at 9:00 P.M. See Figure 2 for interpretation of the code.

1-1-25-1-12

0	12	33	33	33	33	33	33	33	33
0	13	33	33	33	33	33	33	33	33
0	14	33	33	33	33	33	33	33	33
0	15	33	33	33	33	33	33	33	33
0	16	44	44	44	44	44	44	44	44
0	17	33	33	33	33	33	33	33	33
0	18	33	33	33	33	33	33	33	33
0	19	33	33	33	33	33	33	33	33
0	20	44	44	44	44	44	44	44	44

2-2-25-1-12

0	01	37	37	37	33	37	33	38	33
0	02	37	37	37	33	88	37	38	33
0	03	33	33	33	33	33	37	77	37
0	04	36	33	33	33	33	33	33	33
0	06	47	44	11	11	44	44	48	44
0	08	22	33	33	77	77	88	88	77
0	10	33	44	11	33	33	22	38	11

3-1-25-1-24

0	24	33	33	33	33	33	33	33	33
0	25	33	33	33	33	33	33	33	33
0	26	77	77	77	77	77	77	77	77
0	28	33	33	33	33	33	33	33	33
0	29	33	33	33	33	33	33	33	33
0	30	33	33	33	33	33	33	33	33

4-2-25-1-24

0	33	88	88	88	88	88	88	88	88
0	34	88	38	38	38	38	77	77	77
0	35	88	88	88	88	88	88	88	88
0	36	77	77	77	77	77	77	33	77
0	37	88	88	88	88	88	77	88	88
0	40	88	88	88	88	88	88	88	88

5-1-25-1-00

0	41	37	33	37	33	33	37	37	37
0	42	33	33	33	33	33	33	33	33
0	43	11	33	33	36	36	37	37	37
0	44	33	33	33	33	33	33	33	33
0	45	33	33	33	33	33	33	33	33
0	46	33	33	33	33	33	33	33	33
0	47	33	33	33	33	33	33	33	33
0	48	77	37	77	33	33	33	33	33
0	49	36	37	33	33	33	33	33	33

6-2-25-1-00

0	51	33	33	33	33	33	33	33	33
0	52	33	33	33	33	33	33	33	33
0	53	33	33	33	33	33	33	33	33
0	54	33	33	33	33	33	33	33	33
0	55	33	33	33	33	33	33	33	33
0	56	33	33	33	33	33	33	33	33
0	57	55	55	55	33	55	33	55	33
0	58	38	37	33	33	33	33	33	33
0	60	55	55	37	33	55	88	77	33

7-1-10-1-12

1	12		99	99	99	99	77	77	77	88
1	13		99	99	99	99	99	99	99	99
1	14		99	99	99	99	77	88	88	88
1	15		99	99	99	99	88	88	88	88
1	16		99	99	99	99	88	88	88	88
1	17		88	88	88	88	38	88	88	77
1	19		99	99	99	99	77	73	99	99

8-2-10-1-12

1	01		88	99	99	99	99	38	99	99
1	02		38	11	11	11	38	88	88	38
1	03		99	99	99	99	99	88	88	38
1	04		37	37	36	88	88	88	88	88
1	05		88	99	99	99	77	77	88	88
1	06		88	88	88	88	88	88	99	99
1	07		37	88	99	99	38	38	83	83
1	09		77	77	77	77	73	77	77	77
1	10		88	11	11	11	11	11	11	11

9-1-10-1-24

1	21		99	99	99	99	99	99	77	88
0	22		37	37	77	77	77	77	88	88
0	24		38	38	38	33	33	33	33	33
1	25		99	99	99	88	88	77	88	88
0	26	2	88	38	83	11	11	11	77	11
1	27		99	88	99	38	38	38	77	33
1	28		88	77	77	77	77	77	77	77
1	29		88	77	77	77	77	77	88	77
1	30	2	88	88	88	88	88	88	88	88

10-2-10-1-24

1	31		99	99	99	99	99	99	99	99
1	32		99	99	99	99	99	99	99	99
1	33		99	88	88	88	88	88	88	88
1	34		99	88	37	37	37	83	83	83
1	35		99	99	88	88	88	88	88	88
1	36		99	99	88	88	88	88	88	88
1	37		99	99	88	88	99	99	99	99
1	39		88	88	88	88	88	88	88	77
1	40		99	99	88	77	88	88	88	88

11-1-10-1-00

1	41	77	77	77	88	88	88	88	88
1	42	99	99	99	99	99	99	99	99
1	43	99	99	99	99	99	99	99	99
1	44	88	77	77	77	77	77	77	88
1	45	99	99	99	99	99	99	99	99
1	46	88	88	88	88	88	88	88	88
1	47	88	88	88	88	88	88	88	88
1	48	99	99	99	99	99	99	99	99
1	49	77	77	78	88	88	88	88	78

12-2-10-1-00

1	51	99	88	88	88	88	88	88	88
1	52	99	99	99	99	99	99	99	99
1	54	38	38	38	38	38	38	38	38
1	55	93	88	99	88	88	77	88	99
1	53	99	99	99	99	99	99	99	99
1	56	99	99	99	99	99	88	88	99
1	57	99	99	88	99	88	88	88	88
1	59	77	77	77	77	77	77	77	77

13-1-35-1-12

0	62	11	17	17	17	17	17	17	17
0	63	33	55	55	55	55	33	55	37
0	65	33	33	33	33	33	33	33	33
0	66	33	33	33	33	33	33	33	33
0	67	37	33	33	33	33	33	33	37
0	68	33	33	33	33	33	33	33	33
0	69	36	33	33	33	33	33	33	33

14-2-35-1-12

0	70	33	77	77	77	37	33	33	33
0	72	33	33	33	33	33	33	33	33
0	74	33	33	33	33	83	37	37	37
0	75	55	55	55	55	55	55	55	55
0	77	33	33	33	33	77	88	88	88
0	78	33	33	33	38	83	88	37	37

15-1-35-1-24

0	24	33	33	33	33	33	33	33	33
0	25	33	33	33	33	33	33	33	33
0	26	11	11	11	11	11	11	11	11
0	27	33	33	33	33	33	33	33	33
0	28	33	33	33	33	33	33	33	33
0	29	33	77	33	33	33	33	33	33

16-2-35-1-24

0	33	88	88	88	33	38	38	33	33
0	35	37	38	83	83	83	33	83	38
0	36	88	88	88	88	55	77	77	88
0	37	88	88	88	88	88	88	88	38
0	38	88	88	88	83	88	88	83	88
0	40	88	88	88	88	88	88	88	88

17-1-35-1-00

0	41	77	77	33	33	33	37	37	77
0	42	77	77	77	77	88	88	37	37
0	43	88	77	77	77	77	36	77	37
0	44	88	88	88	88	77	77	88	37
0	46	11	11	11	11	11	11	11	11
0	47	88	88	88	88	17	77	33	33
0	49	33	33	33	33	33	33	33	33

18-2-35-1-00

0	80	55	55	55	55	55	77	55	37
0	81	73	88	88	88	88	73	77	88
0	83	55	33	33	33	33	33	33	33
0	84	37	77	77	77	37	37	37	37
0	86	33	33	33	33	33	33	37	33
0	87	55	37	37	55	55	55	33	87

1-1-25-2-12

0	61	33	33	33	33	33	33	33	33
0	63	55	33	33	33	33	33	33	33
0	64	66	33	33	33	33	33	33	33
0	65	33	33	33	33	37	88	88	88
0	66	37	37	33	33	33	33	33	33
0	69	37	33	33	33	88	88	99	88

2-2-25-2-12

0	79	33	33	33	33	33	33	33	33
0	80	33	33	33	33	33	55	66	33
0	81	38	33	33	33	55	33	33	33
0	83	66	11	33	33	33	33	33	33
0	94	77	77	77	37	77	77	77	77
0	87	88	88	88	99	88	88	88	88

3-1-25-2-24

0	22	2	37	37	37	37	33	33	33	33
1	27		99	99	99	99	99	88	88	88
1	28		99	99	99	99	83	58	77	73
0	30	2	33	33	33	33	33	33	33	33
0	32	2	33	88	88	88	33	33	33	33
1	43		99	99	88	88	88	88	88	88

4-2-25-2-24

0	99		81	11	88	88	88	11	55	11
1	98		99	99	88	33	55	88	33	33
1	35		88	99	99	88	11	33	33	11
1	36		88	88	88	88	88	88	88	88
0	37		55	33	38	55	58	38	85	33
0	39	2	88	88	77	33	55	77	33	33

5-1-25-2-00

0	42		88	44	44	33	33	44	44	44
0	46		17	17	17	11	11	11	11	11
0	40		38	37	37	33	33	33	33	33
0	41		88	33	33	33	33	33	33	77
0	43		88	66	55	33	77	55	55	77
0	49		88	88	77	88	11	33	33	38

6-2-25-2-00

0	70		11	33	33	33	33	33	33	33
0	71		33	37	37	33	33	33	33	33
0	72		33	33	33	33	33	33	33	33
0	73		88	33	33	55	33	33	33	37
0	74		88	33	33	33	33	33	33	33
0	75		77	33	33	33	33	33	33	33
0	76		77	33	33	33	33	33	33	33
0	77		33	33	33	33	33	33	33	33

7-1-10-2-12

1	61		38	37	33	33	33	33	33	37
1	62		37	37	33	33	33	33	33	33
1	65	2	88	88	88	88	55	77	77	38
0	63	2	37	37	33	33	33	33	33	33
0	64	2	33	33	33	33	33	33	88	88
0	66	2	36	73	37	37	57	36	33	33
0	67	2	33	33	33	33	55	33	77	88
0	69	2	88	77	76	76	57	77	66	77

8-2-10-2-12

0	79		33	33	33	33	77	33	33	73
0	80		33	33	77	33	73	73	88	99
0	82		37	33	37	77	88	38	88	88
0	83		17	73	73	88	33	33	18	88
0	96		37	33	33	33	37	33	33	33
0	95		37	33	33	33	99	88	88	88

9-1-10-2-24

1	61		88	33	88	38	33	33	77	33
1	63		88	33	77	33	38	38	77	33
1	64		99	33	88	99	99	88	55	88
1	65	2	88	33	88	88	55	88	55	88
1	66		37	33	77	88	66	33	77	38
0	67		77	33	55	77	33	33	37	55
1	68		88	83	88	88	88	77	77	88
1	69		77	88	88	88	88	86	66	66

10-2-10-2-24

0	63		88	33	55	88	77	55	77	73
0	62		88	77	11	11	55	55	33	88
0	66		88	88	33	77	33	33	55	63
0	67		77	88	77	77	77	33	88	88
0	60		88	88	77	77	88	88	88	88
0	51		77	36	77	77	88	73	33	73
0	28		88	33	77	77	77	73	33	77

11-1-10-2-00

0	40		11	33	33	11	33	33	11	33
0	41		77	18	77	77	77	37	37	37
0	43		83	33	37	37	33	33	33	33
0	47		33	17	38	11	33	11	11	33
0	48		73	73	73	73	36	36	36	36
0	49		99	88	88	88	77	77	77	83

12-2-10-2-00

1	70		88	88	88	88	88	88	88	77
1	93		88	88	88	88	88	88	88	88
1	72		88	88	88	88	88	88	38	88
1	73		88	88	88	88	88	88	88	88
1	75		36	88	88	88	38	38	38	36
1	77		73	38	38	38	38	33	36	73

13-1-35-2-12

0	78	37	33	33	88	88	88	88	88
0	99	55	33	33	88	88	88	88	88
0	98	88	33	33	33	88	88	88	88
0	25 2	88	88	88	88	88	88	88	88
0	24 2	55	33	33	33	33	33	33	33
0	22 2	11	11	11	11	11	88	33	11

14-2-35-2-12

0	79	33	33	73	88	88	77	77	33
0	80	33	33	33	33	77	37	33	38
0	82	33	33	33	33	77	88	88	33
0	87	33	33	33	33	88	77	88	88
0	91	33	33	33	33	33	33	88	55
0	92	33	33	33	33	88	88	88	88

15-1-35-2-24

0	32 2	88	88	88	88	88	88	88	88
0	34 2	88	88	88	88	88	88	88	88
0	35 2	37	77	77	77	88	88	88	88
0	37 2	88	88	88	88	88	88	88	88
0	31 2	88	88	88	88	88	99	99	88
0	33	88	88	88	88	88	88	37	33

16-2- 35-2-24

0	34 2	88	88	88	88	88	88	88	88
0	37	88	88	88	88	88	88	88	88
0	21 2	88	88	88	88	88	88	33	88
0	60	88	88	88	88	88	88	88	88
0	51 2	88	88	88	88	88	88	88	88
0	99	99	99	99	99	88	88	88	88

17-1-35-2-00

0	41	88	88	88	58	55	88	88	28
0	51	88	88	55	55	55	77	77	88
0	60	99	88	77	77	77	77	77	88
0	44	38	33	33	11	11	11	33	38
0	45	33	33	33	33	38	33	88	55
0	46	11	11	11	11	11	11	11	11
0	47	77	37	37	33	77	15	33	33
0	48	88	38	33	33	88	38	33	33
0	49	77	33	33	33	33	33	33	33

18-2-35-2-00

0	70		88	33	33	33	33	88	88	38
0	71		37	33	33	33	55	33	33	33
0	73		88	55	55	33	33	33	66	88
0	74	2	77	33	33	77	37	88	55	33
0	75		33	55	55	33	33	55	33	37
0	77		33	33	33	33	33	88	38	33
0	78		66	33	33	33	33	33	33	33

APPENDIX II

COMPUTER PROGRAM USED FOR ANALYSIS OF VARIANCE

```
**    ANALYSIS OF VARIANCE ONEWAY CLASSIFICATION N = N,
     1OR NOT 3/17/66
C     ANALYSIS OF VARIANCE ONEWAY CLASSIFICATION N = N,
     1OR NOT
C     PROGRAMMED BY F J WOJCIK JUNE12, 1964 VA. INST.
     1MAR. SCI.
C     READ FOLLOWING COMMENT CARDS FOR DIRECTIONS FOR
     1RUNNING PROGRAM
C     SUPPLY DATA CARDS WITH NUMBER OF AREAS TO BE PROCESSED
     1(NEAREA)
C     SUPPLY DATA CARDS WITH NUMBER OF OBSERVATIONS IN EACH
     1AREA (N)
C     SUPPLY DATA CARDS WITH FIRST DATA ON ONE AREA, THEN
     1THE NEXT
C     SUPPLY DATA CARDS WITH VALUES OF F (TWO TAILED) TO
     1CHECK VARIANCES
C     F FROM SNEDECOR, P276, TABLE 10.81.1 AT .025 LEVEL
C     SUPP:Y DATA CARD WITH VALUES OF T IF NUMBERS NOT EQUAL
C     TABULAR VALUES OF T FROM TABLE 2.7.1 P46 AT .95 LEVEL
C     TEST DECK 1 YIELDS F = 6.93515 DF 1./18.
C     TEST DECK 2 YIELDS F = 9.59853 DF 5./53
C     TEST DECK 3 YIELDS T = 45.81298 DFT = 8.
C     TEST DECK 4 YIELDS T2 = 4.35277 RECOMPUTED TABULAR
     1T = 2.26206
C          FEED IN DATA FOR TWO AREAS AT A TIME
      DIMENSION EM(20), SX(20), SX2(20),CT(20),VAR(20),
     1VARM(20),X(1200)
      DIMENSION XBAR(20), CX2(20)
    1 TS=0.
      C=0.
      EN=0.
      XAREA=0.
      T2=0.
      DFT=0.
      READ2,NAREA
    2 FORMAT(I4)
      DO10J=1,NAREA
      READ3,N
    3 FORMAT(I4)
      EM(J)=N
      COMPUTE SUM OF SQUARES AND VARIANCES
```

```
    READ4,(X(K),K=1,N)
  4 FORMAT(30X,8(F4.0), 18X)
    SX(J)=0
    SX2(J)=0
    DO20K=1,N
    SX(J)=SX(J)+X(K)
 20 SX2(J)=SX2(J)+(X(K)**2.)
    XBAR(J)=SX(J)/EM(J)
    PRINT6,SX(J),EM(J),XBAR(J)
  6 FORMAT(12H SUM OF X = ,F10.2,5H N = F7.0,8H XBAR =
   1F10.3)
    CT(J)=(SX(J)**2.)/EM(J)
    CX2(J)=SX2(J)-CT(J)
    PRINT7,CX2(J),EM(J)
  7 FORMAT(28H CORRECTED SUM OF SQUARES = ,F14.5,5H N=
   1,F5.0)
    VAR(J)=CX2(J)/(EM(J)-1.)
    PRINT 32,VAR(J)
 32 FORMAT(12H VARIANCE = ,F14.5)
    VARM(J)/EM(J)-1.
    TS=TS+SX2(J)
    C=C+SX(J)
    XAREA=XAREA+((SX(J)**2.)/EM(J))
 10 EN=EN+EM(J)
    CTSS=(C**2.)/EN
    XAREA=XAREA=XAREA-CTSS
    TSS=TS-CTSS
    XMAX=VAR(1)
    XMIN=VAR(1)
    DO30J=1,NAREA
    IF(XMAX-VAR(J))33,34,34
 33 XMAX=VAR(J)
 34 IF(XMIN-VAR(J))30,30,36
 36 XMIN=VAR(J)
 30 CONTINUE
 35 FVAR=XMAX/XMIN
    READ37.P
 37 FORMAT(F6.3)
    IF(FVAR-P)38,39,39
 39 PRINT55
 55 FORMAT(20H FVAR IS SIGNIFIGANT)
 57 IF(NAREA-2)51,51,52
 51 IF(EM(1)-EM(2))61.60,61
 60 T=((XBAR(1)-XBAR(2))*(EM(1)-1.)))/((CX2(1)+CX2(2))**.5)
    DFT=EM(1)-1.
    PRINT 40,T,DFT
    PAUSE
    GO TO 1
 61 T2=(XBAR(1)-XBAR(2))/(VARM(1)-VARM(2))**.5
    READ150,T3,T4
150 FORMAT(F7.4,F7.4)
    DFT2=((VAR(1)*T3)+(VAR(2)*T4))/(VAR(1)+VAR(2))
    PRINT 62,T2,DFT2
 62 FORMAT(6H T2 = ,F10.5,22H RECOMPUTED T VALUE = ,F10.5)
```

```
      PRINT18
      PAUSE
      GO TO 1
   52 PRINT 50
   50 FORMAT(40HERROR N NOT EQUAL TO N MORE THAN 2 AREAS)
      PRINT 56
   56 FORMAT(38H FEED DATA BACK IN TWO AREAS AT A TIME)
      PRINT18
      PAUSE
      GO TO 1
   38 PRINT12
   12 FORMAT(49H FVAR IS NOT SIGNIFIGANT RUN ANALYSIS OF
     1VARIANCE)
      RES=TSS-XAREA
      DFTSS=EN-1.
      DFXAR=NAREA-1
      DFRES=DFTSS-DFXAR
      AREAM=XAREA/DFXAR
      RESM=RES/DFRES
      PRINT13
   13 FORMAT(13x,16H SUM OF SQUARES ,3X,5H DF  4X,13H
     1MEAN SQUARED)
      PRINT14,TSS,DFTSS
   14 FORMAT(10H TOTAL     ,F14.7,7X,F5.0)
      PRINT15,XAREA,DFXAR,AREAM
   15 FORMAT(10H INDIVID  F14.7,7X,F5.0,7X,F14.7)
      PRINT16,RES,DFRES,RESM
   16 FORMAT(/10H RESIDUAL F14.7,7X,F5.0,7X,F14.7)
      F=AREAM/RESM
      PRINT 17,F,DFXAR,DFRES
   17 FORMAT(20X,5H F = ,F14.5,4H DF F5.0,F5.0)
      PRINT18
   18 FORMAT(60H TO PROCESS NEW CASE, LOAD DATA, PUSH START
     1AND READER START
      PAUSE
      GO TO 1
      END
```

Note: This program print-out is for those analyses in which all eight of the readings were used for the read-in data. For those analyses in which the 12:00 noon data only was used, the program was identical with the exception of statement 4 which was changed to

```
   4 FORMAT(30X, 8(F4.0), 18X)
```

APPENDIX III

WITHIN GROUP REGRESSION

The within group regression provides a statistical test of the similarity of the individuals to one another, the strongest correlation being r=1. As often occurs in computer-executed statistical tests, division by zero was directed; the incongruous results* are seen in the correlation values for blinded anoles. In the listings below, the first eighteen correlations are for intact anoles; the second eighteen are for blinded anoles.

Test groups	n	Calculated r^2	Approximated r
1	9	1.00	1
2	7	1.00	1
3	6	1.00	1
4	6	0.99	1
5	9	1.00	1
6	9	infinity*	-
7	7	0.91	0.97
8	9	0.85	0.92
9	9	1.00	1
10	9	0.99	1
11	9	1.00	1
12	8	1.00	1
13	7	anomoly	-
14	6	1.00	1
15	6	1.00	1
16	6	1.00	1
17	7	4.11	2
18	6	anomoly	-

Test groups	n	Calculated r^2	Approximated r
1	6	infinity*	-
2	6	infinity	-
3	6	infinity	-
4	6	infinity	-
5	6	infinity	-
6	8	infinity	-
7	8	infinity	-
8	6	infinity	-
9	8	infinity	-
10	7	infinity	-
11	6	infinity	-
12	6	infinity	-
13	6	infinity	-
14	6	infinity	-
15	6	infinity	-
16	6	anomoly	-
17	9	anomoly	-
18	7	anomoly	-

Note: By inspection of the individual means and coefficients of the test animals within these groups, it is apparent that these results are due to a lack of significant variation of the anoles' color responses with time.

VITA

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